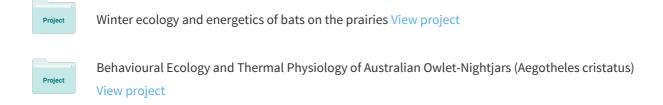
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VARIATION IN HABITAT USE AND PREY SELECTION BY YUMA BATS, MYOTIS YUMANENSIS

R. M. BRIGHAM, H. D. J. N. ALDRIDGE, AND R. L. MACKEY

Department of Biology, University of Regina, Regina, Saskatchewan, Canada S4S 0A2 (RMB) Agricultural and Food Research Council, Polaris House, North-star Ave., Swindon, United Kingdom SN2 1UH (HDJNA) Division of Ecology, Department of Biological Sciences, University of Calgary, Calgary, Alberta, Canada T2N 1N4 (RLM)

The purpose of our study was to assess variation in habitat use and prey selection by *Myotis yumanensis* in British Columbia. In particular we tested the hypothesis that habitat use and resulting prey choice are constant among different reproductive and age classes. We light tagged 115 individuals and observed their foraging activity for a total of 218 min on 16 nights from May to September 1989. The four reproductive and age classes (pregnant, lactating, post-lactating, juvenile) all predominantly foraged within open, uncluttered habitats over land and low over water. Dietary variation suggests this species forages opportunistically on aquatic insects with changes in diet reflecting changes in availability.

Key words: Myotis, habitat use, prey, British Columbia

Recently investigators of insectivorous bat communities have attempted to make ecological inferences about the relationship between wing morphology and feeding ecology (Aldridge and Rautenbach, 1987; Crome and Richards, 1988; McKenzie and Rolfe, 1986; O'Shea and Vaughan, 1980). Interspecific differences in wing morphology have been used to successfully predict habitat use and dietary differences by insectivorous bats (e.g., Aldridge and Rautenbach, 1987). However, studies of morphologically similar species illustrate that habitat use and diet may be similar or different (Aldridge, 1986; Aldridge and Rautenbach, 1987; Barclay, 1991; Saunders and Barclay, in press). It is often assumed that the habitat use and resulting prey choice are relatively constant among different reproductive and age classes of the same species. There are few data on the foraging behavior of insectivorous bats that address this assumption. The purpose of this study was to assess variation in habitat use and prey selection by different reproductive and age classes of Myotis yumanensis. Ontogenetic improvement of flight abilities in juveniles complicate matters (Buchler, 1980), since their limited neuromuscular development may restrict them to uncluttered habitats (sensu Fenton, 1990) until flight abilities improve to the extent that they can forage in the same habitats as adults.

Myotis yumanensis is a small (5–9 g) insectivorous bat found in arid areas of western North America (van Zyll de Jong, 1985). Morphologically it is similar to M. lucifugus, to the extent that hybridization was thought to occur (Herd and Fenton, 1983). Herd and Fenton (1983) observed this species foraging predominantly over flowing water, and rarely above 10 m; however, the low aspect ratio and wing loading suggest this species should be able to exploit cluttered habitats. Major dietary items reported include Trichoptera, Ephemeroptera (Herd

and Fenton, 1983), Diptera, Lepidoptera, and Coleoptera (Whitaker et al., 1977).

MATERIALS AND METHODS

Field work was conducted 29 May-9 September 1989. We caught 168 individual M. yumanensis as they emerged from a maternity colony in an abandoned warehouse near Oliver (49°10′N, 119°37′W) in the Okanagan Valley of British Columbia. We identified the bats based on van Zyll de Jong (1985) and Herd and Fenton (1983). Adult females were characterized as either pregnant (by palpation), lactating (by the expression of milk from a nipple), or post-lactating (bare patches around the nipples, but no milk expression). Juveniles were distinguished from adults by the lack of ossification of the metacarpal-phalangeal joint on the third digit (Racey, 1974).

We assessed habitat use by bats of a particular age or reproductive class (pregnant, lactating, post-lactating, or juvenile) on 16 nights by observing the flight of light-tagged foraging individuals (Aldridge and Rautenbach, 1987; Buchler, 1976). We affixed gelatin capsules filled with Cyalume® (American Cyanamid Company, Milton, FL) to the dorsal or ventral surface of the bat with surgical adhesive. Light tags were affixed to only one reproductive or age class on any given night. Observations of where bats flew were continuously described into voice-note recorders and later transcribed to determine the number of seconds spent by each bat in each habitat type. The study area was divided into seven habitat types or foraging zones, ranked subjectively by the degree of clutter and the dominant substrate type (Aldridge and Rautenbach, 1987). The habitat zones ranged, in increasing order of complexity, from open spaces lacking obstacles (zone one) to highly cluttered spaces within the foliage of trees (zone seven).

On all but one night, bats carrying light tags were released 100 m from the colony on the bank of the Okanagan River. On the other night we released bats at the precise capture site to confirm that the foraging sites we observed bats using on the other nights were typical and not a consequence of where they had been released. Foraging sequences were only included in the analysis if they lasted 10 s or longer and bats appeared to be foraging.

We analyzed the light-tagging data in two ways. First, the time spent by all bats on any given night in each zone was used to calculate the hab-

itat-use index (equation 4.1 from Aldridge and Rautenbach, 1987). The index reflects the average complexity of the habitats used by foraging bats. A higher value indicates that proportionately more time was spent in more cluttered zones. We compared the index values between nights and between the different reproductive and age classes.

We also compared habitat use directly between nights and between the different reproductive and age classes of bats by using a repeated-measures analysis of variance (ANOVA). For this analysis each observation of a light-tagged bat on any given night was treated separately. Despite the variation in the duration of observation sequences, all activity data were weighted equally. This prevented habitat-use measures from being weighted by data from long sequences when bats foraged in relatively open habitats (e.g., over water) where they were easier to observe. We used a repeated-measures ANOVA because it takes into account that our observations were not necessarily independent. For all statistical tests we used a rejection level of 0.05, and where variances were unequal or the data were non-normal, nonparametric tests were used.

On 12 of the nights when light-tagging took place, we spread collecting sheets below roosting sites inside the warehouse to collect fecal samples for diet analysis. We analyzed a total of 20 randomly selected pellets from each night's sample or as many as were collected if <20. The insect remains were identified to order, and for each pellet the percent volume comprised by each order was estimated (Whitaker, 1988).

RESULTS

We released 115 light-tagged M. yumanensis and recorded 177 foraging sequences totalling 13,063 s (218 min). Bats concentrated their foraging in uncluttered areas (zone one), low over water (zone two), or close to trees (zone four; Table 1). Some individuals also foraged low over pasture (zone three).

The habitat-use indices were not significantly different among the four classes (Kruskal-Wallis F = 2.67, df = 3, P > 0.05). Because bats spent <0.5% of the total observation time in habitats five, six, and seven, these zones were excluded from further analyses. Bats did not spend equal pro-

Table 1.—Habitat use by pregnant, lactating, post-lactating, and juvenile Myotis yumanensis in British Columbia, showing time (s) spent in each habitat and the mean habitat-use index (n is the number of bats released with light tags, and n_0 is the number of sequences recorded).

	n/n _o	Total time _ (s)	Habitats							Mean habitat- use
Class			1	2	3	4	5	6	7	index
Pregnant	31/25	2,903	266	1,910	26	701	0	0	0	2.40
Lactating	9/14	974	115	551	11	295	0	2	0	2.51
Post-lactating	37/77	3,863	917	2,625	54	262	3	0	2	1.92
Juvenile	38/61	5,323	1,559	2,826	161	754	14	6	3	2.04
Total	115/177	13,063	2,857	7,912	252	2,012	17	8	5	2.12

portions of their time in foraging zones one, two, three, and four (arcsine transformed proportions), reflecting the heavy use of zones one and two throughout the summer (F = 101.0, d.f. = 3, P < 0.001). There was no significant zone-by-class interaction (F = 1.81, d.f. = 9 and 24, P > 0.05), indicating that the four age and reproductive classes of M. yumanensis used the four habitat types in the same manner.

We could not determine the age or reproductive class of the individuals from whom we collected fecal pellets. However, since we found no evidence for variation in habitat use through time, we assume that the insects whose remains were found in fecal pellets were captured in the same habitats. The diet composition, in terms of prey taxa, did change among nights ($\chi^2 = 140.3$, P < 0.01; Fig. 1). After 2 July, trichopterans and dipterans (mostly chironomids) comprised the majority of the diet.

DISCUSSION

Our results support the assumption that the degree of clutter associated with foraging habitats of *M. yumanensis* does not vary significantly among reproductive and age classes. However, several potentially complicating factors must be taken into account. Based on the wing morphology of *M. yumanensis* (low wing loading and aspect ratio), we would have predicted that this species would spend a large proportion of its foraging time in cluttered habitats (Aldridge and Rautenbach, 1987; Norberg and Ray-

ner, 1987). Although, as Fenton (1990) pointed out, bats with wings adapted for cluttered areas are not precluded from foraging in open habitats. We suggest that at our study site, *M. yumanensis* forages in relatively open habitats because of high prey abundance. Insect abundance over the Okanagan River near our study site remains consistently high after 1 June (Brigham, 1990).

From an energetic standpoint, there are advantages for aerial insectivores concentrating their activities in open habitats since the stringent demands of slow-maneuverable flight are relaxed (Aldridge and Rautenbach, 1987; Norberg and Rayner, 1987). Foraging in uncluttered zones low over water or land also reduces flight costs due to the ground effect (Aldridge, 1989). Thus, even for bats such as M. yumanensis, which are morphologically adapted for slow maneuverable flight in cluttered situations, foraging in cluttered zones should occur only when the prey density in those zones is greater than that encountered in open habitats by an amount necessary to increase net energy intake.

Due to the nature of habitat use by M. yumanensis in our study, the ability to rigorously address the assumption of variation among classes of individuals is limited. A female bat's mass may vary by >30% during the summer, resulting from pregnancy, paturition, and prehibernatory fattening. Changes in mass will have direct effects on wing loading (Norberg and Rayner, 1987)

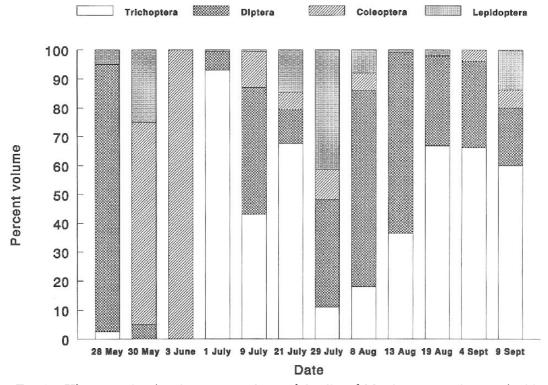


Fig. 1.—Histogram showing the percent volume of the diet of *Myotis yumanensis* comprised by each insect order for each sample date.

and should have significant effects on maneuverability (Aldridge and Brigham, 1988), which should in turn necessitate changes in foraging behavior. We expected that pregnant bats with relatively high wing loadings should be restricted to foraging in less cluttered habitats than lactating individuals. However, since bats of all reproductive classes in our study foraged in open habitats, the predicted shift could not occur. Therefore, a further test of the assumption is required using a clutter-adapted species like *M. yumanensis*, but in a situation where foraging in clutter occurs regularly.

Our data suggest that the ontogenetic development of flight in juvenile *M. yumanaensis* is relatively unimportant in determining foraging-habitat selection. This contradicts the observation by Herd and Fenton (1983) of *M. yumanensis* shifting to more open habitats at the time when young bats begin foraging flights. However, the use

of relatively open uncluttered habitats by all classes of bats at this site again makes detecting the predicted shift difficult.

The dietary variation we found suggests that M. yumanensis forage opportunistically (sensu Fenton and Morris, 1976) and harvest prey from swarms of aquatic insects. The primarily aquatic-insect diet is consistent with the fact that the majority of foraging time was spent in the over-water habitat. The changes in the diet we found through the summer may simply reflect changes in swarm composition. Brigham (1990) found that after 1 June at a site 10 km north of the present study site, chironomids and trichopterans were the most abundant insects over the Okanagan River. Our data, which show that these insects were the most important prey types for M. yumanensis, support the opportunistic-foraging hypothesis.

Unfortunately, we could not directly test

the assumption that the diet was similar for the four reproductive and age classes, because we did not collect fecal pellets from a known class of bats on nights when lighttagging occurred. However, our finding that the different classes use the same foraging habitats provides circumstantial evidence that diet should be similar for the different classes. Further, since overall diet appears to vary with insect availability, any differences in diet between classes may only reflect differences in availability rather than actual differences in prey selection by the bats.

In conclusion, although our data support the assumption that aerial insectivorous bats of different reproductive and age classes use the same habitats over long periods of time, a further test of this assumption is required at a site where insect abundance is relatively low and adults presumably spend more time foraging in cluttered habitats. Our study does provide some evidence that predicting habitat use by a species based on wing morphology alone is not feasible. If M. yumanensis is typical, clutter-adapted species will readily forage in open habitats when prey is abundant.

Acknowledgments

We acknowledge the field assistance of R. M. R. Barclay, J. L. Graves, R. Hampton, C. G. Harris, A. L. MacKinlay, P. W. Morgan, H. N. Matthews, and M. B. Saunders. L. D. Harder provided valuable statistical assistance. We thank the behavioural ecology lunch group, M. B. Fenton, M. B. Saunders, J. R. Speakman, and J. O. Whitaker, Jr., for their constructive comments and the Okanagan-Similkameen Cooperative Growers Association for access to the colony. The work was supported by a short-term research grant from the University of Calgary, a Natural Sciences and Engineering Researh Council (NSERC) Postdoctoral fellowship to RMB, and NSERC operating grants to R. M. R. Barclay.

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Submitted 15 July 1991. Accepted 25 September 1991.